



## Change in plant spatial patterns and diversity along the successional gradient of Mediterranean grazing ecosystems

Concepción L. Alados<sup>a,\*</sup>, Ahmed ElAich<sup>b</sup>, Vasilios P. Papanastasis<sup>c</sup>, Huseyin Ozbek<sup>d</sup>,  
Teresa Navarro<sup>e</sup>, Helena Freitas<sup>f</sup>, Mihalis Vrahnakis<sup>c</sup>,  
Driss Larrosi<sup>b</sup>, Baltasar Cabezudo<sup>e</sup>

<sup>a</sup> Pyrenean Institute of Ecology, Montañana Ave. 177, P.O. Box 202, 50080 Zaragoza, Spain

<sup>b</sup> Department Production Animal, Institute Agronomique et Veterinaire Hassan II, Rabat, Morocco

<sup>c</sup> Laboratory of Rangeland Ecology, Aristotle University, 54006 Thessaloniki, Greece

<sup>d</sup> Department Soil Science, Çukurova University, Adana, Turkey

<sup>e</sup> Department Vegetal Biology, Málaga University, 29080 Málaga, Spain

<sup>f</sup> Department Botany, Coimbra University, Portugal

Received 4 April 2003; received in revised form 12 September 2003; accepted 27 October 2003

### Abstract

In this study, we analyze the complexity of plant spatial patterns and diversity along a successional gradient resulting from grazing disturbance in four characteristic ecosystems of the Mediterranean region. Grazing disturbance include not only defoliation by animals, but also associated disturbances as animal trampling, soil compaction, and mineralization by deposition of urine and feces. The results show that woodland and dense matorral are more resistant to species loss than middle dense and scattered matorral, or grassland. Information fractal dimension declined as we moved from a dense to a discontinuous matorral, increasing as we moved to a more scattered matorral and a grassland. In all studied cases, the characteristic species of the natural vegetation declined in frequency and organization with grazing disturbance. Heliophyllous species and others with prostrate or rosette twigs increased with grazing pressure, particularly in dense matorral. In the more degraded ecosystem, only species with well-adapted traits, e.g., buried buds or unpalatable qualities showed a clear increase with grazing. Indeed, the homogeneity of species distribution within the plant community declined monotonically with grazing impact. Conversely, the spatial organization of the characteristic plants of each community increased in the better-preserved areas, being also related to the sensitivity of the species to grazing impact. The degree of autocorrelation of plant spatial distribution at the species level and the information fractal dimension at the community level allow us to quantify the degree of degradation of natural communities and to determine the sensitivity of key species to disturbance.

© 2004 Elsevier B.V. All rights reserved.

**Keywords:** Fractal analysis; Grazing systems; Spatial patterns

\* Corresponding author. Tel.: +34 97 67 16113; fax: +34 9767 16019.

E-mail address: [alados@ipe.csic.es](mailto:alados@ipe.csic.es) (C.L. Alados).

**Nomenclature:** The scientific names of species are according to Flora Europaea (Tutin et al., 1972) and Med. Checklist (Greuter et al., 1984–89).

## 1. Introduction

Ecosystems consist of multiple populations of different taxa interacting in a non-linear way with each other and with the environment. Ecosystems are complex, dynamic, open systems maintained by external input of energy (Jørgensen, 1982) moving in a self-organizing way by choosing the best pathway offered to move far from the thermodynamic equilibrium (Jørgensen, 2000). Disturbance of the ecosystem will alter the dynamics of the interacting species, moving the system away from the state of equilibrium, to which the ecosystem may return after perturbation (Emlen et al., 1998). The system will become unstable until a new equilibrium develops. The transition state will be less energetically efficient than the natural evolved one (Emlen et al., 1998). Thus, ecosystem preservation must be based on the capacity of the ecosystem to maintain its functions and organization after regular disturbances (Müller et al., 2000; Gunderson and Holling, 2001). Understanding the mechanism of ecosystem preservation requires two main components of interpretation: (i) the extent of perturbation the ecosystem can undergo and still remain in the same stage; (ii) the capacity of the system to self-organize and adapt.

Spatial interactions in natural plant communities may produce emergent patterns at larger spatial scales (Kolasa and Pickett, 1991; Martens et al., 2000; Peterson, 2000). These patterns can be analyzed along, for instance, successional gradients to study the adaptation of ecosystems to changed conditions. Plant spatial patterns are the result of processes operating at different spatial scales and may respond to changed conditions such as water availability (Couteron and Lejeune, 2001; Rietkerk et al., 2002a, b). Spatial patterns can also arise as a consequence of interaction among individuals, generating a zone of influence that affects the surrounding space (Wu et al., 1985). For example, during the early process of colonization, random distribution of plants is commonly observed (Kershaw, 1963; Fowler, 1990). As the interactions among the system components develop, the system moves away

from randomness to a more ordered spatial organization (Aarssen and Turkington, 1985; Soro et al., 1999). These regularities represent “attractors” of the dynamics, indicating some kind of equilibrium state at the community level. Although the constant immigration of species triggers a number of non-linear processes that constraints the stability of the ecosystem (Solé et al., 2002), allowing its constant evolution.

Mediterranean grazing systems are complex systems whose sustainability (ability to maintain structure and function “indefinitely”, Costanza et al., 1992) depends not only on the grazing impact, but also on the history of grazing (Whittaker, 1977; Milchunas and Lauenroth, 1993) and soil nutrients availability (Proulux and Mazumder, 1998). Grazing disturbance includes not only plant defoliation by animals and alteration of the competitive/facilitative interaction (Huston, 1994) but also soil compaction and destruction of plants by animal trampling and acceleration of the nutrient cycling with the plant–soil system altering the nutrient balance (Proulux and Mazumder, 1998). Recent simulation model analyses found that grazing optimization is possible and depends on recycling efficiencies and the depletion abilities of plant community composition (Mazancourt and Loreau, 2000). Indeed, the “intermediate disturbance” hypothesis (Connell, 1978; Sousa, 1984) postulated that intermediate levels of disturbance favor maximal biodiversity, which can be explained as a result of the release from competition in resource-rich ecosystems (Grime, 1979). On the contrary, in semiarid grazing ecosystems, irreversible vegetation changes may occur when herbivore number is high in grazing managed systems in comparison with self-regulating natural systems (Van de Koppel and Rietkerk, 2000). Thus, the relation between grazing impact and ecosystem functioning is complex and what role species diversity plays in determining ecosystem function remains unanswered (Keeley and Swift, 1995; Troumbis and Memtsas, 2000).

Determining long-term patterns of spatial variation and the factors, which cause them are key research needs in community ecology. Quantifying such patterns will increase our ability to predict the response of the communities to both natural and anthropogenic environmental change. Fractal-dimension analysis may provide a scale-related measure of spatial patterns and can therefore be used to describe and understand pattern in species diversity (Allen and

Starr, 1982; Ritchie and Olff, 1999). A change in the fractal dimension of plant spatial patterns may reflect ongoing directional change in biological and physical processes in the community. In a previous study, we presented an evidence that grazing disturbance in semiarid Mediterranean ecosystems leads to a decline in species diversity and an increase in the heterogeneity of species frequency distribution at the same time that it increases the unpredictability (randomness) of plant spatial distribution (Alados et al., 2003). In this study, we are interested in knowing if the change in plant spatial patterns in response to grazing disturbance observed in a semiarid matorral is maintained along a Mediterranean climatic gradient from semiarid steppes to sub-humid woodlands.

According with self-organization instability theory (Solé et al., 2002), the exponent  $z$  of the species–area relation (SAR,  $S = \alpha A^z$ ) decreases when the relative importance of the interaction within the system increases with respect to immigration.  $S$  is the total number of species observed within a given area  $A$ . As a result, we expect that species distribution be more homogeneous ( $z$  declines) when: (i) interaction within the system declines, such as occurrence in well-developed ecosystems close to the equilibrium (Berlow, 1999); (ii) immigration increases due to colonization of empty space by species adapted to disturbance in highly disturbed ecosystems (Grime, 1979). In contrast, at the level of the characteristic species of each community, we expect a monotonic decline in spatial organization with disturbance.

## 2. Methods

### 2.1. Study area and data collection

Four characteristic ecosystems of the Mediterranean region were selected. Two different areas were selected from southern Spain: A sub-humid woodland; *Quercus suber* forest (925 mm of average rainfall and 17.5 °C of mean annual temperature), located at 600 m a.s.l., Sierra de las Nieves Natural Park (Bornoque, Málaga) and a scattered matorral (scrubland) of *Chamaerops humilis* L. and *Periploca laevigata* Aiton (200 mm of average rainfall and 18 °C of mean annual temperature) located at 100 m a.s.l., Cabo de Gata Natural Park (Almería). Grazing management in these areas

involved their use by single shepherds holding grazing rights. The animals (sheep and goats) move daily from the shelter to different parts of the rangeland, producing a gradient of soil and vegetation disturbance out to the periphery. A dense matorral of *Phillyrea* and *Pistacia* located at 50 m a.s.l. (590 mm of average rainfall and 16.2 °C of mean annual temperature) was selected from the Sithonia peninsula, northern Greece (Toroni, Chalkidiki). Grazing management was similar to the Spanish sites, although the land was communal, not private as in Spain, and the grazing animals were only goats. A high mountain grassland located at 1900 m a.s.l. (800 mm of average rainfall and 22 °C of mean annual temperature) in the territory of the Ait Beni Yacoub, Middle Atlas (Morocco) grazed by sheep, was also included. Traditional activity in this area was nomadic.

A grazing gradient was established in each study area at increasing distance from the water point (for the nomadic herds) or from the shelter (for the established herds). In S. Nieves (Spain), Sithonia (Greece) and Middle Atlas (Morocco), three levels of grazing pressure were identified, namely low, medium and high. In C. Gata (Spain), an ungrazed treatment was also added. Effective stocking rate (individual ha<sup>-1</sup> year<sup>-1</sup>) was calculated for each study area by direct rangeland observations (Table 1). Animal movements (sheep and goats) were located with GPS and transferred to a map in a GIS (geographical information system) format. Effective stocking rate was calculated as the average stocking rate multiplied by the percentage of time each grazing site is used.

In order to analyze the effect of grazing impact on vegetation spatial patterns, the line intercept method (every 20 cm) was applied to 39 random 500 m transects (three per grazing treatment and site). Vegetation surveys were conducted during periods of peak vegetation cover (April to June) in 2000. A total number of 158 vascular plant species were observed in the study area of S. Nieves, 96 species in Sithonia peninsula, 144 in C. Gata, and 95 in the Middle Atlas study area.

### 2.2. Data analysis

The Shannon diversity index (Shannon and Weaver, 1949) measures the complexity of the system, and represents the information,  $I(\epsilon)$ , necessary to character-

Table 1

Effective stocking rate (ind. ha<sup>-1</sup> year<sup>-1</sup> using the study area), richness (average number of species  $\pm$  S.E.), percentage of bare-ground and means  $\pm$  S.E. of the Shannon and Evenness indexes calculated from the presence of species along the three transects per test area

Grazing pressure	Effective stocking rate	Richness	Bareground cover (%)	Shannon index	Evenness index
Forest of Sierra de las Nieves (Spain)					
Low	0.27	56.7 $\pm$ 3.5 <sup>a</sup>	4.5	2.42 $\pm$ 0.04 <sup>a</sup>	0.597 $\pm$ 0.007 <sup>a</sup>
Medium	0.53	86 $\pm$ 2.3 <sup>b</sup>	4.6	2.87 $\pm$ 0.03 <sup>b</sup>	0.644 $\pm$ 0.004 <sup>a</sup>
High	1.20	55.7 $\pm$ 6.1 <sup>a</sup>	28.6	2.57 $\pm$ 0.15 <sup>a</sup>	0.640 $\pm$ 0.020 <sup>a</sup>
		$F_{2,6} = 16.32^{**}$	$G = 1003.1^{***}$	$F_{2,6} = 6.35^*$	$F_{2,6} = 4.51$
Shrubland of Sithonia Peninsula (Greece)					
Low	0.3	59 $\pm$ 2.6 <sup>a</sup>	4.4	2.90 $\pm$ 0.05 <sup>a</sup>	0.713 $\pm$ 0.007 <sup>a</sup>
Medium	2.6	61.7 $\pm$ 0.3 <sup>a</sup>	16.4	2.80 $\pm$ 0.04 <sup>a</sup>	0.679 $\pm$ 0.010 <sup>ab</sup>
High	8.2	62.3 $\pm$ 0.9 <sup>a</sup>	21.5	2.73 $\pm$ 0.05 <sup>a</sup>	0.658 $\pm$ 0.010 <sup>b</sup>
		$F_{2,6} = 1.18$	$G = 489.3^{***}$	$F_{2,6} = 3.49$	$F_{2,6} = 8.98^*$
Scrubland of Cabo de Gata (Spain)					
Ungrazed	0	89.7 $\pm$ 4.5 <sup>a</sup>	20.9	3.03 $\pm$ 0.10 <sup>a</sup>	0.674 $\pm$ 0.016 <sup>a</sup>
Low	0.27	53 $\pm$ 2.9 <sup>b</sup>	34.6	2.34 $\pm$ 0.09 <sup>b</sup>	0.589 $\pm$ 0.016 <sup>b</sup>
Medium	0.46	51.66 $\pm$ 3.3 <sup>b</sup>	31.5	2.12 $\pm$ 0.06 <sup>b</sup>	0.537 $\pm$ 0.012 <sup>b</sup>
High	0.65	54 $\pm$ 4.6 <sup>b</sup>	29.1	1.64 $\pm$ 0.07 <sup>c</sup>	0.411 $\pm$ 0.010 <sup>c</sup>
		$F_{3,8} = 22.52^{***}$	$G = 115.9^{***}$	$F_{3,8} = 46.10^{***}$	$F_{3,8} = 62.43^{***}$
Grasslands of the Middle Atlas (Morocco)					
Low	0.9	61.5 $\pm$ 4.5 <sup>a</sup>	9.4	2.61 $\pm$ 0.12 <sup>a</sup>	0.668 $\pm$ 0.003 <sup>a</sup>
Medium	1.54	44.5 $\pm$ 0.5 <sup>b</sup>	21	2.20 $\pm$ 0.06 <sup>b</sup>	0.603 $\pm$ 0.009 <sup>b</sup>
High	2.49	36 $\pm$ 0.99 <sup>c</sup>	20	1.60 $\pm$ 0.06 <sup>c</sup>	0.447 $\pm$ 0.015 <sup>c</sup>
		$F_{2,6} = 33.38^{**}$	$G = 171.9^{***}$	$F_{2,6} = 36.28^{***}$	$F_{2,6} = 127.70^{***}$

$F$  values calculated from the one-way ANOVA with grazing pressure as fixed effect factors. Means with different letters are significant at the 0.05 level, DHS Tukey contrast.

\*  $P < 0.05$ .

\*\*  $P < 0.01$ .

\*\*\*  $P < 0.0001$ .

ize the state of the system within an accuracy of  $\varepsilon$  (Shannon, 1948).  $I(\varepsilon) = \sum_{i=1}^{N(\varepsilon)} p_i \ln 1/p_i$ ;  $p_i$  is the probability of occurrence of the  $i$ th of  $N(\varepsilon)$  events. In our case,  $p_i = x_i / \sum_{N(\varepsilon)} x_i$ , where  $x_i$  is the frequency of contacts of the species ( $i$ ) in each transect of size ( $\varepsilon$ ). When all the events have equal probability,  $p_i = 1/N(\varepsilon)$  then  $I(\varepsilon) = I_{\max}(\varepsilon) = \ln N(\varepsilon)$ . The ratio  $I(\varepsilon)/I_{\max}(\varepsilon) = J$  is called the evenness index (Pielou, 1966; Frontier, 1987). The probability that a given plant species occupies in a given transect depends on that transect's size, i.e.,  $N(\varepsilon)$  changes with transect (window) size ( $\varepsilon$ ). Consequently,  $I(\varepsilon)$  also changes.

Diversity indices are scale-dependent, i.e., they change with the size of the area sampled. We need to characterize the complexity of the ecosystem indepen-

dently of the scale, at least within a range of scales. Fractal dimension provides a quantitative measure independent of the scale.

The information fractal dimension (Farmer et al., 1983) is calculated by regressing  $I(\varepsilon)$  against the natural logarithm of  $\varepsilon$ . The slope of the line is the information fractal dimension:

$$D_I \cong \lim_{\varepsilon \rightarrow 0} \frac{I(\varepsilon)}{\ln 1/\varepsilon}$$

We calculated  $I(\varepsilon)$  at a series of scales of size  $\varepsilon = 2^n$ , for  $n$  from 0 to 6. The curve-fitting accuracy of this relationship is very high ( $R^2$  is  $0.997 \pm 0.0003$ ,  $n = 39$ , for the whole dataset) showing that the scale of magnification chosen accurately represents the scale at which the processes were acting. As we increase the window

size to more than 128 m, the fitting accuracy starts to decline. In consequence, we maintained window size between 1 and 64 m.

Because we obtained the information fractal dimension from lineal transects, the values obtained are constrained to lie between 0 and 1. The information fractal dimension declines from a homogeneous and random scattered plant distribution to an aggregated plant distribution (Li, 2000).

The level of spatial autocorrelation of individual plant species was calculated by the Detrended Fluctuation Analyses (DFA), developed by Peng et al. (1992) and applied to plant spatial analyses by Alados et al. (2003). DFA quantifies the degree of organization of each plant species, i.e., random or non-random distribution. The method is a modification of the root-mean square analyses of a random walk (Wang and Uhlenbeck, 1945). This method is similar to the semi-variogram (Legendre and Legendre, 1998) but has the advantage that it removes local trends and consequently, is not affected by non-stationarities, i.e., systematic change in the mean. It measures the level of autocorrelation ( $\alpha$ ) of a random walk ( $y(s) = \sum_{i=1}^s z(i)$ ) generated from the sequence of presence ( $z(i) = +1$ ) and absence ( $z(i) = -1$ ) intercepts per each species along the transect. We calculated the residual variance of the regression of  $y_b(s)$  on  $s$  per non-overlapping boxes of size  $b$  from the  $N$  point contacts in the transect:  $F^2(b) = \sum_{s=1}^N (y_b(s) - \hat{y}_b(s))^2 / N$ . The slope of the line relating  $F(b)$  to  $b$  determines the scaling exponent  $\alpha$ :  $F(b) \propto b^\alpha$ . The scaling exponent  $\alpha$  is inversely related to the fractal dimension. When average crown size is lower than intercept intervals, a shuffle of the data set gives values of  $\alpha = 1/2$ , indicating no correlation in the sequence (white noise), while  $\alpha \neq 1/2$  indicates a long-range power-law correlation (plant distribution sequence depends on the spatial history of the distribution). In order to remove spatial autocorrelation obtained from species with crown cover larger than the size of the intercept interval, we calculated the  $\alpha$  value of simulated randomizations of individual plants. Comparisons between the actual plant distribution and the random distribution were performed for the most abundant species in each community and assessed by  $t$ -test. Comparisons between the observed alpha values of each treatment were calculated separately for each species by bootstrap procedure with 1000 random re-analyses.

### 3. Results

#### 3.1. Changes in plant diversity with grazing

The number of species declined significantly with grazing pressure in the semiarid scattered matorral of C. Gata and in the mountain grassland of Middle Atlas. No significant effects were observed in the dense matorral of Sithonia, while a significant richness increase was observed at the medium grazing level at the S. Nieves woodland. As expected, percentage of bare-ground increased with grazing pressure in all the study areas (Table 1).

Shannon diversity index, which is a measure of information flow across the ecosystem, was measured at the scale of the 500 m transect. It declined significantly with increased grazing in the scattered matorral of C. Gata (in comparison with ungrazed, DHS Tukey contrast) and the grassland of Middle Atlas (Table 1), while the difference was not significant for the dense matorral of Sithonia. S. Nieves, on the other hand, showed a significant diversity increase under medium-grazing pressure (DHS Tukey contrast).

The evenness index represents the homogeneity of species distribution within the plant community. A high evenness index indicates that all species are equally represented. As the evenness index declined, dominance of some species over others appeared. The evenness index declined significantly with grazing impact in all the studied sites, except in S. Nieves woodland (Table 1).

#### 3.2. Fractal dimension of plant spatial patterns

The information fractal dimension provides a quantitative measure of the degree of patchiness of the plant community independent of scale. It increases with increases in the degree of randomness (lack of spatial correlation). Grazing significantly reduced the fractal dimension of plant distribution in the S. Nieves woodland ( $F_{2,6} = 49.49$ ,  $P < 0.001$ ) as the vegetation changed from dense to middle dense matorral, and in Sithonia ( $F_{2,6} = 7.55$ ,  $P = 0.02$ ) from low to medium grazing pressure as the matorral became discontinuous. When we moved to a more scattered vegetation, at the heavy grazing matorral of Sithonia and semiarid matorral of C. Gata formation, the information fractal dimension increased with grazing disturbance as the plant distri-

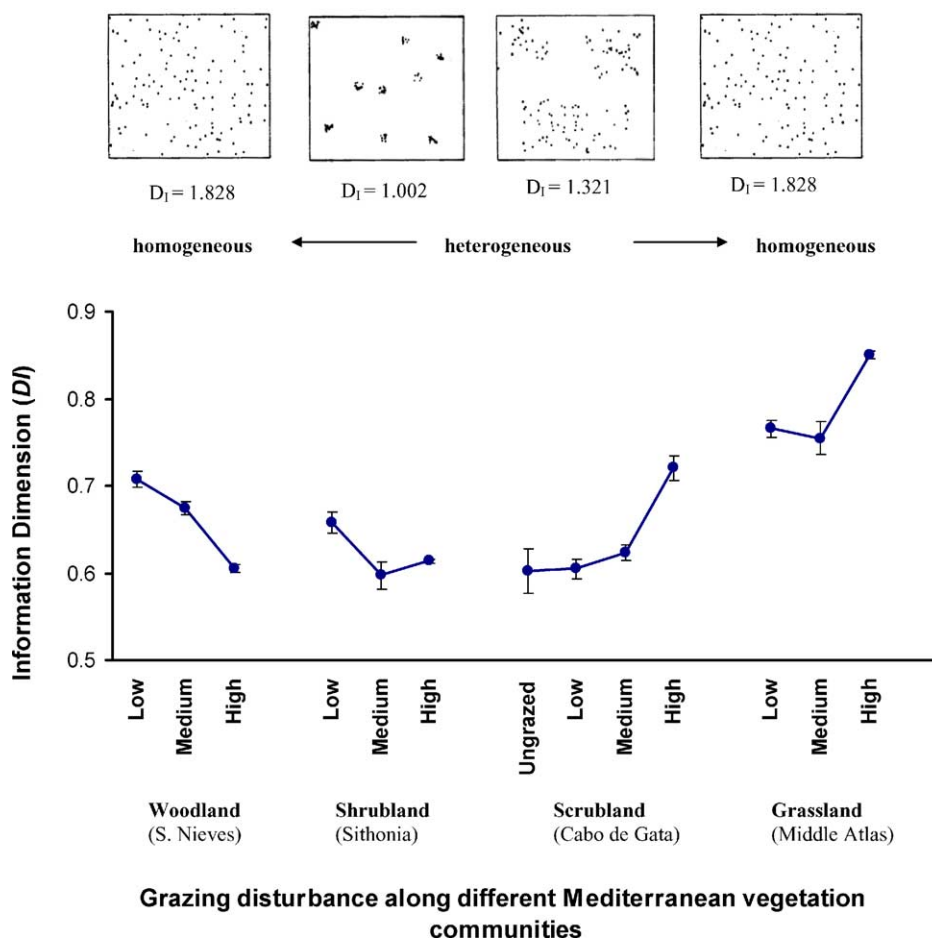


Fig. 1. Changes on information fractal dimension ( $D_I$ ) along the grazing disturbance of different Mediterranean communities. Information fractal dimension for random, aggregated and random clumped point patterns from the upper part of the figure were obtained from Li (2000).

bution became more sparse ( $F_{3,8} = 11.87$ ,  $P = 0.003$ , in C. Gata). This occurred also in the grassland formation ( $F_{2,6} = 17.9$ ,  $P = 0.003$ , in the Middle Atlas; Fig. 1).

Spatial autocorrelation analyses revealed that, in general, annual plants were more randomly distributed (lower alphas) than woody species (larger alpha values, i.e., more organized distribution). Overall, most of the species exhibited a spatial autocorrelation that differed significantly from a random distribution (Table 2). The significance of the  $t$ -test comparing average alpha values from the actual distributions with those from the random distributions was significant in most cases.

The characteristic species of the sclerophyllous *Quercus suber* L. forest of S. Nieves (*Juniperus oxycedrus* and *Erica arborea*), became more organized (larger al-

pha values) at low or median grazing pressure. Tree species such as *Q. suber* and *Pinus pinaster*, although declining in frequency, did not change their spatial distribution, keeping the same alpha values along the grazing gradient. Other species, such as *Calicotome villosa* (Poir.) Link and *Cistus ladanifer* also become more randomly distributed with grazing perturbation. Finally, early succession, heliophyllous species, e.g., *Phlomis purpurea*, favored by woodland gaps, became clumped (larger alpha values) as they colonized open gaps.

The least grazing-resistant shrubland species of the *Sithonia dense matorral*, *Quercus coccifera* and *Olea europea* var. *sylvestris*, became significantly more random with grazing impact. Overall, most of the species



Table 2

Means  $\pm$  S.E. ( $n$ )  $\alpha$  values of the scaling exponent alpha from the equation  $F(b) \propto b^\alpha$ , of the most abundant species along the grazing disturbance of different vegetation communities

Species	Low	Medium	High	$F$	$\alpha$ -Random
Woodland of Sierra de las Nieves (Spain)					
<i>Adenocarpus telonensis</i>	0.704 $\pm$ 0.02 (3)*	0.592 $\pm$ 0.05 (3)	0.567 $\pm$ 0.03 (3)	4.47	0.522 $\pm$ 0.01 (9)
<i>Astragalus lusitanicus</i>	–	0.811 $\pm$ 0.04 (3)*	0.662 $\pm$ 0.04 (3)*	0.003	0.521 $\pm$ 0.01 (6)
<i>Brachypodium retusum</i>	–	0.924 $\pm$ 0.0 (3)*	0.827 $\pm$ 0.00 (1)*	1.765	0.618 $\pm$ 0.01 (4)
<i>Calicotome villosa</i>	0.733 $\pm$ 0.01 (3)*	0.723 $\pm$ 0.05 (3)*	0.513 $\pm$ 0.02 (2)	12.59**	0.507 $\pm$ 0.02 (8)
<i>Cistus albidus</i>	0.606 $\pm$ 0.05 (3)*	0.704 $\pm$ 0.07 (3)*	0.703 $\pm$ 0.03 (3)*	1.22	0.525 $\pm$ 0.01 (9)
<i>Cistus ladanifer</i>	0.819 $\pm$ 0.01 (3)*	0.798 $\pm$ 0.01 (3)	0.729 $\pm$ 0.01 (3)	14.56**	0.729 $\pm$ 0.02 (9)
<i>Cistus monspeliensis</i>	0.766 $\pm$ 0.00 (1)*	0.639 $\pm$ 0.05 (2)*	0.700 $\pm$ 0.02 (3)*	2.75	0.522 $\pm$ 0.01 (6)
<i>Cistus salvifolius</i>	0.692 $\pm$ 0.07 (3)*	0.665 $\pm$ 0.01 (2)*	0.636 $\pm$ 0.02 (3)*	0.39	0.524 $\pm$ 0.01 (8)
<i>Dactylis glomerata</i>	0.625 $\pm$ 0.02 (3)*	0.659 $\pm$ 0.03 (3)*	0.585 $\pm$ 0.04 (3)*	1.57	0.513 $\pm$ 0.01 (9)
<i>Erica arborea</i>	0.818 $\pm$ 0.07 (3)*	0.937 $\pm$ 0.03 (3)*	0.573 $\pm$ 0.01 (3)	15.29**	0.602 $\pm$ 0.02 (9)
<i>Genista umbellata</i>	0.619 $\pm$ 0.02 (3)*	0.673 $\pm$ 0.02 (3)*	–	2.23	0.517 $\pm$ 0.01 (6)
<i>Juniperus oxycedrus</i>	0.763 $\pm$ 0.02 (3)*	0.825 $\pm$ 0.01 (3)*	0.726 $\pm$ 0.01 (3)*	13.75**	0.627 $\pm$ 0.01 (9)
<i>Lavandula stoechas</i>	0.704 $\pm$ 0.02 (3)*	0.719 $\pm$ 0.01 (3)*	0.722 $\pm$ 0.02 (3)*	0.25	0.536 $\pm$ 0.01 (9)
<i>Phillyrea angustifolia</i>	0.696 $\pm$ 0.02 (3)*	0.722 $\pm$ 0.03 (2)*	0.657 $\pm$ 0.03 (3)*	1.95	0.579 $\pm$ 0.01 (11)
<i>Phlomis purpurea</i>	0.623 $\pm$ 0.01 (3)*	0.802 $\pm$ 0.01 (3)*	0.783 $\pm$ 0.01 (3)*	61.13**	0.501 $\pm$ 0.01 (9)
<i>Pinus pinaster</i>	0.987 $\pm$ 0.01 (3)*	0.972 $\pm$ 0.03 (3)*	0.966 $\pm$ 0.02 (3)*	0.21	0.827 $\pm$ 0.01 (9)
<i>Pistacia lentiscus</i>	0.793 $\pm$ 0.04 (2)*	0.631 $\pm$ 0.09 (3)	0.625 $\pm$ 0.14 (2)	0.86	0.545 $\pm$ 0.03 (7)
<i>Quercus suber</i>	0.981 $\pm$ 0.01 (3)	1.016 $\pm$ 0.02 (3)	1.005 $\pm$ 0.04 (3)	0.34	0.868 $\pm$ 0.05 (11)
<i>Ulex parviflorus</i>	0.692 $\pm$ 0.00 (1)*	0.756 $\pm$ 0.03 (3)*	0.671 $\pm$ 0.05 (3)*	1.34	0.516 $\pm$ 0.01 (7)
Dense matorral of Sithonia Peninsula (Greece)					
<i>Anthoxanthum odoratum</i>	0.727 $\pm$ 0.23 (3)*	0.685 $\pm$ 0.02 (3)*	0.697 $\pm$ 0.02 (3)*	0.963	0.523 $\pm$ 0.00 (9)
<i>Avena barbata</i>	0.677 $\pm$ 0.02 (3)*	0.634 $\pm$ 0.02 (3)*	0.596 $\pm$ 0.02 (3)*	3.692	0.511 $\pm$ 0.01 (9)
<i>Carex sp.</i>	0.738 $\pm$ 0.02 (3)*	0.659 $\pm$ 0.03 (2)	–	6.689**	0.541 $\pm$ 0.00 (5)
<i>Calicotome villosa</i>	0.694 $\pm$ 0.02 (3)*	0.670 $\pm$ 0.05 (3)*	0.636 $\pm$ 0.07 (3)	0.352	0.566 $\pm$ 0.00 (9)
<i>Cistus monspeliensis</i>	0.849 $\pm$ 0.01 (3)	0.796 $\pm$ 0.03 (3)*	0.778 $\pm$ 0.03 (3)*	1.870	0.682 $\pm$ 0.00 (9)
<i>Cynosurus echinatus</i>	0.698 $\pm$ 0.03 (3)*	0.653 $\pm$ 0.01 (3)*	0.584 $\pm$ 0.02 (3)*	6.532*	0.505 $\pm$ 0.01 (9)
<i>Daucus carota</i>	0.697 $\pm$ 0.04 (3)	0.680 $\pm$ 0.01 (3)*	0.604 $\pm$ 0.00 (1)*	0.895	0.511 $\pm$ 0.00 (7)
<i>Dactylis glomerata</i>	0.682 $\pm$ 0.01 (3)*	0.651 $\pm$ 0.02 (3)*	0.658 $\pm$ 0.02 (3)*	0.879	0.535 $\pm$ 0.00 (9)
<i>Lagurus ovatus</i>	0.703 $\pm$ 0.00 (3)*	0.664 $\pm$ 0.03 (3)*	0.623 $\pm$ 0.03 (3)*	4.159	0.527 $\pm$ 0.00 (9)
<i>Leontodon tuberosus</i>	0.668 $\pm$ 0.01 (3)*	0.589 $\pm$ 0.03 (2)	0.536 $\pm$ 0.03 (3)	7.464*	0.514 $\pm$ 0.00 (8)
<i>Olea europaea</i> var. <i>sylvestris</i>	0.792 $\pm$ 0.01 (3)*	0.808 $\pm$ 0.02 (3)*	0.705 $\pm$ 0.03 (3)	6.306*	0.637 $\pm$ 0.00 (9)
<i>Phillyrea latifolia</i>	0.746 $\pm$ 0.01 (3)*	0.738 $\pm$ 0.04 (3)*	0.763 $\pm$ 0.05 (3)*	0.142	0.626 $\pm$ 0.00 (9)
<i>Pistacia lentiscus</i>	0.896 $\pm$ 0.01 (3)	0.876 $\pm$ 0.02 (3)*	0.835 $\pm$ 0.02 (3)*	3.305	0.651 $\pm$ 0.00 (9)
<i>Plantago bellardi</i>	0.656 $\pm$ 0.01 (3)*	0.631 $\pm$ 0.03 (3)*	0.699 $\pm$ 0.02 (3)*	2.206	0.540 $\pm$ 0.01 (9)
<i>Poa bulbosa</i>	0.597 $\pm$ 0.02 (3)	0.569 $\pm$ 0.01 (2)	0.736 $\pm$ 0.03 (2)*	13.721*	0.532 $\pm$ 0.00 (7)
<i>Quercus coccifera</i>	0.921 $\pm$ 0.01 (3)*	0.881 $\pm$ 0.06 (3)*	0.632 $\pm$ 0.03 (3)	16.633*	0.599 $\pm$ 0.00 (9)
<i>Stipa bromoides</i>	0.640 $\pm$ 0.04 (3)*	0.758 $\pm$ 0.07 (3)*	0.541 $\pm$ 0.05 (3)	3.430*	0.531 $\pm$ 0.00 (9)
<i>Vulpia muralis</i>	0.648 $\pm$ 0.00 (3)*	0.600 $\pm$ 0.04 (3)*	0.636 $\pm$ 0.00 (3)*	1.019	0.505 $\pm$ 0.01 (9)

Table 2 (Continued)

Species	Ungrazed	Low	Medium	High	<i>F</i>	$\alpha$ -Random
Scattered matorral of Cabo de Gata (Spain)						
<i>Ballota hirsuta</i>	0.658 ± 0.03 (3)*	0.684 ± 0.01 (3)*	0.657 ± 0.03 (2)*	0.663±0.04 (3)*	0.17	0.593±0.01 (6)
<i>Brachypodium distachyon</i>	0.715 ± 0.05 (3)*	0.674 ± 0.03 (3)*	0.664 ± 0.02 (2)*	0.649±0.04 (3)*	0.53	0.519±0.02 (12)
<i>Brachypodium retusum</i>	0.892 ± 0.02 (3)*	0.618 ± 0.04 (3)*	0.750 ± 0.01 (2)*	0.689±0.03 (3)*	16.15**	0.665±0.09 (6)
<i>Chamaerops humilis</i>	0.893 ± 0.02 (3)*	0.886 ± 0.03 (3)*	0.870 ± 0.02 (2)*	0.863±0.02 (3)*	0.43	0.760±0.01 (6)
<i>Genista spartioides</i>	0.907 ± 0.06 (3)*	0.733 ± 0.03 (3)*	0.786 ± 0.03 (2)	0.676±0.00 (1)	3.74	0.613±0.02 (3)
<i>Helianthemum almeriense</i>	0.707 ± 0.07 (3)*	0.677 ± 0.02 (3)	-	0.479±0.00 (1)	1.94	0.523±0.01 (6)
<i>Launaea lanifera</i>	0.718 ± 0.04 (3)*	0.686 ± 0.05 (3)*	0.696 ± 0.05 (2)*	0.677±0.04 (3)*	0.15	0.532±0.02 (6)
<i>Lavandula multifida</i>	0.678 ± 0.04 (3)*	0.640 ± 0.02 (3)	0.552 ± 0.01 (2)*	0.503±0.01 (2)	7.40*	0.590±0.05 (10)
<i>Lycium intricatum</i>	0.693 ± 0.02 (3)*	0.689 ± 0.02 (2)*	0.764 ± 0.01 (2)*	0.687±0.07 (3)	0.47	0.566±0.01 (6)
<i>Periploca laevigata</i>	0.863 ± 0.01 (3)*	0.803 ± 0.04 (3)*	0.827 ± 0.02 (2)*	0.671±0.02 (3)	11.31**	0.719±0.01 (4)
<i>Phlomis purpurea</i>	0.782 ± 0.02 (3)*	0.626 ± 0.03 (3)*	0.741 ± 0.04 (2)	0.660±0.03 (3)*	5.44*	0.579±0.01 (7)
<i>Plantago bellardi</i>	0.715 ± 0.04 (3)*	0.539 ± 0.03 (2)	0.690 ± 0.04 (3)*	0.583±0.01 (3)*	5.71*	0.513±0.01 (6)
<i>Salsola genistoides</i>	0.703 ± 0.02 (3)*	0.602 ± 0.02 (2)	0.689 ± 0.00 (1)	0.710±0.00 (1)	3.38	0.631±0.01 (6)
<i>Sideritis oxeosylla</i>	0.697 ± 0.02 (2)*	0.699 ± 0.06 (3)*	0.729 ± 0.05 (2)*	0.617±0.04 (3)	0.97	0.591±0.02 (10)
<i>Stipa tenacissima</i>	0.865 ± 0.01 (3)*	0.738 ± 0.02 (3)	0.808 ± 0.00 (2)*	0.826±0.05 (3)*	3.71	0.705±0.02 (14)
<i>Thymus hyemalis</i>	0.719 ± 0.02 (3)*	0.712 ± 0.02 (3)*	0.659 ± 0.05 (2)*	0.659±0.02 (3)*	1.57	0.518±0.01 (8)
Species	Low	Medium	High	<i>F</i>	$\alpha$ -Random	
Grassland of Middle Atlas (Morocco)						
<i>Carex divisa</i>	0.779 ± 0.05 (3)*	0.816 ± 0.06 (3)*	0.731 ± 0.02 (3)*	0.842	0.552 ± 0.01 (9)	
<i>Cerastium gibralicum</i>	0.701 ± 0.00 (3)*	0.546 ± 0.00 (1)	0.557 ± 0.01 (2)*	133.313*	0.519 ± 0.01 (6)	
<i>Convolvulus cantabricus</i>	0.712 ± 0.15 (2)*	0.624 ± 0.14 (3)*	0.517 ± 0.02 (2)	1.237	0.520 ± 0.01 (7)	
<i>Dactylis glomerata</i>	0.761 ± 0.12 (2)*	0.563 ± 0.06 (2)	0.601 ± 0.03 (3)*	2.168	0.523 ± 0.01 (7)	
<i>Euphorbia nicaeensis</i>	0.619 ± 0.02 (2)	0.585 ± 0.02 (3)	0.774 ± 0.09 (3)*	3.043	0.556 ± 0.01 (8)	
<i>Festuca sp.</i>	0.705 ± 0.01 (3)*	0.546 ± 0.01 (3)	-	219.088**	0.522 ± 0.01 (6)	
<i>Genista pseudopilosa</i>	0.712 ± 0.04 (3)*	0.665 ± 0.04 (3)*	0.743 ± 0.01 (3)*	1.388	0.583 ± 0.01 (9)	
<i>Phleum phleoides</i>	0.704 ± 0.05 (3)*	0.602 ± 0.07 (3)*	0.542 ± 0.06 (3)	1.749	0.497 ± 0.01 (9)	
<i>Poa bulbosa</i>	0.669 ± 0.02 (3)*	0.718 ± 0.03 (3)*	0.674 ± 0.00 (1)*	1.663	0.571 ± 0.01 (9)	
<i>Stipa parviflora</i>	0.733 ± 0.03 (3)*	0.760 ± 0.03 (3)*	0.674 ± 0.03 (3)*	1.844	0.535 ± 0.01 (9)	
<i>Thymelea glomerata</i>	0.546 ± 0.02 (3)	0.671 ± 0.03 (2)*	0.622 ± 0.00 (1)	5.229	0.521 ± 0.01 (6)	
<i>Thymus sp.</i>	0.644 ± 0.02 (3)*	0.640 ± 0.03 (3)*	0.548 ± 0.01 (3)*	6.416	0.510 ± 0.01 (8)	

F-test is performed among the grazing treatment. The significance levels are calculated by bootstrap after 1000 reanalyses.  $\alpha$ -values with \* are significantly different (*t*-test) from the  $\alpha$ -Random, obtained after shuffling data set.

\*  $P < 0.05$ .

\*\*  $P < 0.01$ .



became randomly distributed as the dense matorral was transformed into a discontinuous matorral, with the exception of grazing-resistant species such as *Phillyrea latifolia* that maintained its spatial distribution and *Poa bulbosa*, which became clumped in the open gaps.

A decline in the alpha exponent with grazing was also observed in characteristic species of the C. Gata matorral, e.g., *Periploca laevigata*, *Phlomis purpurea*, *Brachypodium retusum*, and *Lavandula multifida* L., while *Chamaerops humilis* did not change its spatial distribution as a result of grazing, and neither did *Ballota hirsuta*. On the other hand, *Stipa tenacissima*, which favored by grazing disturbance, did not change the degree of randomization in response to grazing (Table 2), becoming the dominant species at the end of the regressive succession (*Stipa steppe*) that results from grazing pressure in the most scattered matorrals.

Finally, grazing favored the randomization of the characteristic colonizing species of the grassland of Middle Atlas, like *Cerastium gilbralicum* and *Thymus* sp., and most perennial grasses like *Festuca* sp., although the difference was not always significant.

## 4. Discussion

### 4.1. Change in plant diversity with grazing

Richness declined with grazing pressure in the most disturbed sites. Nevertheless, in the better preserved sites like S. Nieves woodland, moderate grazing opens gaps, allowing the establishment of shade intolerant and pioneer species like *Phlomis purpurea* and *Lavandula stoechas*. A non-significant variation in plant diversity was observed in the Sithonia shrubland due to the replacement of the species sensitive to grazing (e.g., *Quercus coccifera*, *Olea europaea* var. *sylvestris*) by species with well-adapted traits, e.g., prostrate or rosette twigs (*Plantago* sp.) or buried buds (*Poa bulbosa*; Noy-Meir et al., 1989; Lavorel et al., 1998). Other studies have also reported that moderate levels of disturbance maximize species diversity (Grime, 1979; Connell, 1978; Crawley, 1983; Milchunas et al., 1988; Huston, 1994) to the point that a reestablishment of diversity has been attributed to bison grazing in

grasslands anthropogenically stressed by frequent fires (Collins et al., 1998). Although, when disturbance is very intense, few species can persist, resulting in lower diversity. Indeed, we observed that plants tend to be equally represented (larger evenness index) in the lightly grazed areas in comparison with areas with heavy grazing pressure. Under heavy grazing pressure, a few species dominated the community. For example, cushion perennial grasses with underground stems e.g., *Stipa tenacissima*, with their buried buds are more protected from grazing than shrubs (Hendrickson and Briske, 1997), increasing its relative frequency with grazing pressure from 27% at the control site to 66% at the heavy grazing site. Thus, the C. Gata middle dense scrubland of *Chamaerops*, *Rhamnus* and *Periploca* is transformed progressively into *Stipa* steppe at the end of the regressive succession (Tomaselli, 1981).

In the dense matorral of the Sithonia Peninsula, grazing led to a preponderance of species adapted to high disturbance (*Cistus monspeliensis*) over species indicative of the pristine matorral, such as *Quercus coccifera* and *Olea europaea* var. *sylvestris* that declined 88 and 70%, respectively, becoming very scarce. At the same time, species with grazing syndrome (prostrate or rosette twigs) (Lavorel et al., 1998), e.g., *Plantago* sp. became frequent. In the Middle Atlas grassland, *Poa bulbosa* (a biennial grass with a short growth cycle and a high production of bulblets) dominated under heavy grazing while *Genista* declined by 73%.

### 4.2. Fractal dimension of plant spatial patterns

Because species diversity is the result of processes acting at various spatial and temporal scales, we ideally should study diversity at the scale at which the processes operate. The fractal dimension of structural ecosystem components is an emergent property (or measure) that may reflect the scale at which spatial interactions between these components operate (Allen and Holling, 2002). The information fractal dimension provides is a quantitative measure of the degree of patchiness of the plant community independent of scale, and increases as the degree of randomness (lack of spatial correlation) increases. We found that the information fractal dimension declined as we moved from a dense matorral to a discontinuous matorral.

When we turned from a discontinuous matorral to a scattered matorral, the information fractal dimension increased and kept increasing as we moved to the grasslands. This change in the fractal dimension may indicate a substantial change in the processes that generate plant spatial patterns (Krummel et al., 1987; Sugihara and May, 1990; Li, 2000). The results are in accordance with our expectations and the theory of self-organized instability, that hypothesize that ecological complexity results from the interaction between the trend to increase diversity as ecosystem develops and the negative feedback aroused from interactions among individuals (Solé et al., 2002). Resulting two opposite processes (interaction declining with ecosystem development and immigration increasing with degradation) in a common pattern, i.e., small patches homogeneously distributed into the landscape.

Two hypotheses have been outlined to explain the plant spatial patterns observed in arid and semiarid areas: (i) they are the result of pre-existing environmental heterogeneity (Rietkerk et al., 2002a, b); (ii) they are the result of spatial self-organization caused by water infiltration into vegetated ground (Rietkerk et al., 2002a, b). Recent empirical (Pugnaire et al., 2003) and theoretical studies (HilleRisLambers et al., 2001) have demonstrated that soil infiltration and nutrient retention occurring around the plant crown are responsible for facilitation processes in semiarid vegetation (Bertness and Callaway, 1994; Pugnaire et al., 1996). In contrast, soil erosion and run-off increase when vegetation cover decreases (Elwell and Stocking, 1976). As a result, a positive feedback between reduced plant growth and reduced water and nutrient availability is triggered (Rietkerk and Van de Koppel, 1997) and can thereby contribute to irreversible vegetation destruction, as for example observed in the Sahel, where increases in grazing pressure resulted in irreversible shifts between vegetation states (Le Houérou, 1989).

Spatial organization of the characteristic species of each community increased in the better preserved areas, while as grazing pressure increased, those plants become more randomly distributed except species typical of perturbed ecosystems, which increased their spatial organization, e.g., *Euphorbia* in the middle Atlas grasslands. The degree of increase in randomness with grazing disturbance was related to the sensitivity of the species to grazing impact. Tree species (*Quercus suber* and *Pinus pinaster*) although declining in fre-

quency, did not change their spatial organization. Similarly, the spatial distribution of *Chamaerops*, because its renewal buds are buried and not reachable by live-stock, was not affected by grazing. *Phillyrea latifolia*, which also maintains part of its renewal buds above the height accessible to goats (Sirkou et al., 2003), was also very resistant to heavy grazing. In contrast, sensitive species of the pristine matorral community like *Q. coccifera*, *O. europaea* var. *sylvestris*, *Erica arborea*, *Phlomis purpurea* and even the grazing tolerant *Periploca laevigata* showed a drastic decline in spatial organization.

In addition, we observed that stochasticity declined in the more competitive species, i.e.,  $\alpha$  was lower in the less competitive species (annuals) and larger in the more competitive species (shrubs). According to Tilman's model (1994), stochasticity increases through the competitive hierarchy. The poorer competitors are affected not only by the stochasticity of their colonization and mortality but also by the stochasticity and mortality of the better competitors (Lehman and Tilman, 1997).

In summary, fractal analysis of plant spatial patterns provides a quantitative characterization of the dynamics of plant spatial patterns in response to disturbance, allowing us to predict the effect of grazing independently of scale and determine the sensitivity of key species to grazing disturbance. Changes in the parameters that characterize the vegetation spatial patterns revealed important changes in the processes driving the system, and reflect the switch from one community to the other, demonstrating their efficiency to detect when the structure and function of an ecosystem change drastically and disturbance exceeds the threshold of tolerance. These results agree with previous studies (Alados et al., 2003) and with the hypothesis that plant spatial patterns are the result of spatial self-organization processes (Rietkerk et al., 2002a, b) under the constraints of other processes such as spatial interaction among individuals (Li, 2000).

Recent studies have demonstrated plant spatial-pattern formation as a result of different process using different kind of models, ranging from analytical models (HilleRisLambers et al., 2001), Markov chains (Balzter, 2000; Logofet and Lesnaya, 2000), cellular automata (Bak et al., 1988; Solé and Manrubia, 1995). All these models are limited by the fact that they can not include all the variability of the system into the model

(Whilhelm and Brüggemann, 2000). Nevertheless scaling relations and fractal provide a powerful analytical framework that includes the structural complexity of plant communities and can be used to analyze “emergent patterns” of the ecosystem to predict catastrophic shifts before the ecosystem has moved into the new dynamic state.

## Acknowledgments

The work was performed under the DRASME (Desertification Risk Assessment in Silvopastoral Mediterranean Ecosystems) collaborative research project and CICYT (Evaluación de la presión ganadera para la conservación de las estepas y matorrales Mediterráneos, project number AMB1998-1017). DRASME is funded by the EC under its INCO-DC programme, contract number ERBIC18-CT98-0392. The support from both programs is gratefully acknowledged. We are grateful to John Emlen, Carl Freeman and Bai-Lian Li for critically reading and helpful suggestions on the manuscript. Software for data analysis was developed by Juan Escós.

## Appendix A. Supplementary data

Supplementary data associated with this article can be found at doi:10.1016/j.ecolmodel.2003.10.034.

## References

- Aarssen, L.W., Turkington, R., 1985. Vegetation dynamics and neighbour associations in pasture-community evolution. *J. Ecol.* 73, 585–603.
- Alados, C.L., Pueyo, Y., Giner, M.L., Navarro, T., Escós, J., Barroso, F., Cabezudo, B., Emlen, J.M., 2003. Quantitative characterization of the regressive ecological succession by fractal analysis of plant spatial patterns. *Ecol. Model.* 163, 1–17.
- Allen, T.F.H., Starr, B., 1982. *Hierarchy: Perspectives for Ecological Complexity*. University of Chicago Press, Chicago.
- Allen, C.R., Holling, C.S., 2002. Cross-scale structure and scale breaks in ecosystems and other complex systems. *Ecosystems* 5, 315–318.
- Bak, P., Tang, C., Wiesenfeld, K., 1988. Self-organized criticality. *Phys. Rev. A* 38, 364–374.
- Balzer, H., 2000. Markov chain models for vegetation dynamics. *Ecol. Model.* 126, 139–154.
- Berlow, E.L., 1999. Strong effects of weak interactions in ecological communities. *Nature* 398, 330–334.
- Bertness, M.D., Callaway, R.M., 1994. Positive interactions in communities. *Tree* 9, 191–193.
- Collins, S.L., Knapp, A.K., Briggs, J.M., Blair, J.M., Steinauer, E.M., 1998. Modulation of diversity by grazing and mowing in native tall grass prairie. *Science* 280, 745–747.
- Connell, J.H., 1978. Diversity in tropical rain forests and coral reefs. *Science* 199, 1302–1310.
- Costanza, R., Norton, B.G., Haskell, B.D., 1992. *Ecosystem Health: New Goals for Environmental Management*. Island Press, Washington, DC.
- Couteron, P., Lejeune, O., 2001. Periodic spotted patterns in semiarid vegetation explained by a propagation-inhibition model. *J. Ecol.* 89, 616–628.
- Crawley, M.J., 1983. *Herbivory, the Dynamics of Animal-Plant Interactions*. University of California Press, Berkeley.
- Elwell, H.A., Stocking, M.A., 1976. Vegetal cover to estimate soil erosion hazard in Rhodesia. *Geoderma* 15, 61–70.
- Emlen, J.M., Freeman, D.C., Mills, A., Graham, J.H., 1998. How organisms do right things: the attractor hypothesis. *Chaos* 8, 717–726.
- Fowler, N.L., 1990. Disorderliness in plant communities: comparisons, causes and consequences. In: Grace, J.B., Tilman, D. (Eds.), *Perspectives on Plant Competition*. Academic Press, Inc., San Diego, USA, pp. 291–306.
- Frontier, S., 1987. Applications of fractal theory to ecology. In: Legendre, P. (Ed.), *NATO ASI Series*, vol. G14. Springer-Verlag, Berlin, Heidelberg, pp. 335–378.
- Greuter, W.R., Burdet, H.M., Long, G., 1984–89. *Med-Checklist. Conservatoire et Jardin Botaniques, Genève*.
- Grime, J.P., 1979. *Plant strategies and Vegetation Processes*. John Wiley, New York.
- Gunderson, L., Holling, C.S., 2001. *Panarchy: understanding transformations in human and natural systems*. Island Press, Washington, DC.
- Hendrickson, J.R., Briske, D.D., 1997. Axillary bud banks of two semiarid perennial grasses: occurrence, longevity, and contribution to population persistence. *Oecologia* 110, 584–591.
- HilleRisLambers, R., Rietkerk, M., Van den Bosch, F., Prins, H.H.T., De Kroon, H., 2001. Vegetation pattern formation in semiarid grazing systems. *Ecology* 82, 50–61.
- Huston, M.A., 1994. *Biological Diversity: the Coexistence of Species on Changing Landscapes*. Cambridge University Press, Cambridge.
- Jørgensen, S.E., 1982. A holistic approach to ecological modeling by application of thermodynamics. In: Mitsch, W.J., Ragade, R.W., Bosserman, R.W., Dillon, J.A. (Eds.), *Energetics and Systems*. Ann Arbor Science, Ann Arbor, Michigan.
- Jørgensen, S.E., 2000. General outline of thermodynamic approaches to ecosystems theory. In: Jørgensen, S.E., Müller, F. (Eds.), *Handbook of Ecosystem Theories and Management*. Lewis Publishers, Boca Raton, USA, pp. 113–133.
- Keeley, J.E., Swift, C.C., 1995. Biodiversity and ecosystem functioning in Mediterranean-climate California. In: Davis, G.W., Richardson, D.M. (Eds.), *Mediterranean-type Ecosystems: the*

- Function of Biodiversity. Springer, Berlin, Heidelberg New York, pp. 121–184.
- Kershaw, K.A., 1963. Pattern in vegetation and its causality. *Ecology* 44, 377–388.
- Kolasa, K., Pickett, S.T.A., 1991. Heterogeneity in Ecological Systems. *Ecological Studies* 86. Springer, p. 332.
- Krummel, J.R., Gardner, R.H., Sugihara, G., O'Neill, R.V., Coleman, P.R., 1987. Landscape patterns in a disturbed environment. *Oikos* 48, 321–324.
- Lavorel, S., Touzard, B., Lebreton, J.-D., Clément, B., 1998. Identifying functional groups for response to disturbance in an abandoned pasture. *Acta Oecol.* 19, 227–240.
- Legendre, P., Legendre, L., 1998. *Numerical Ecology*. Elsevier Science B.V., Amsterdam, The Netherlands.
- Le Houérou, H.N., 1989. The grazing land ecosystem of the African Sahel. *Ecological Studies*, vol. 75. Springer-Verlag.
- Lehman, C.L., Tilman, D., 1997. Competition in spatial habitats. In: Tilman, D., Kareiva, P. (Eds.), *Spatial Ecology: The role of Space in Population Dynamics and Interspecific Interactions*. Princeton University Press, Princeton, New Jersey, pp. 185–203.
- Li, B.L., 2000. Fractal geometry applications in description and analysis of patch patterns and patch dynamics. *Ecol. Model.* 132, 33–50.
- Logofet, D.O., Lesnaya, E.V., 2000. The mathematics of Markov models : what Markov chains can really predict in forest successions. *Ecol. Model.* 126, 285–298.
- Martens, S.N., Breshears, D.D., Meyer, C.W., 2000. Spatial distribution of understory light along the grassland/forest continuum: effects of cover, height, and spatial pattern of tree canopies. *Ecol. Model.* 126, 79–93.
- Mazancourt, C., Loreau, M., 2000. Effect of herbivory and plant species replacement on primary production. *Am. Nat.* 155, 735–754.
- Milchunas, D.G., Lauenroth, W.K., 1993. Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecol. Monogr.* 63, 327–366.
- Milchunas, D.G., Sala, O.E., Lauenroth, W.K., 1988. A generalized model of the effect of grazing by large herbivores on grasslands community structure. *Am. Nat.* 130, 168–198.
- Müller, F., Hoffman-Kroll, R., Wiggering, H., 2000. Indicating ecosystem integrity-theoretical concepts and environmental requirements. *Ecol. Model.* 130, 13–23.
- Noy-Meir, I., Gutman, M., Kaplan, Y., 1989. Responses of Mediterranean grassland plants to grazing and protection. *J. Ecol.* 77, 290–310.
- Peng, C.K., Buldyrev, S.V., Goldberger, A.L., Havlin, S., Sciortino, F., Simons, M., Stanley, H.E., 1992. Long-range correlations in nucleotide sequences. *Nature* 356, 168–170.
- Peterson, G.D., 2000. Scaling ecological dynamics: self-organization, hierarchical structure, and ecological resilience. *Climatic Change* 44, 291–309.
- Pielou, E.C., 1966. Species-diversity and pattern-diversity in the study of ecological succession. *J. Theor. Biol.* 10, 370–383.
- Proulx, M., Mazumder, A., 1998. Reversal of grazing impact on plant species richness in nutrient-poor vs. nutrient-rich ecosystems. *Ecology* 79, 2581–2592.
- Pugnaire, F.I., Haase, P., Puigdefábregas, J., 1996. Facilitation between higher plant species in a semiarid environment. *Ecology* 77, 1420–1426.
- Pugnaire, F.I., Armas, C., Valladares, F., 2003. Quantifying plant interactions in a semiarid community. *Oikos*.
- Rietkerk, M., Van de Koppel, J., 1997. Alternate stable states and threshold effects in semiarid grazing systems. *Oikos* 79, 69–76.
- Rietkerk, M., Ouedraogo, T., Kumar, L., Sanou, S., Langevelde, F., Kiema, A., Van de Koppel, J., Van Andel, J., Hearne, J., Skidmore, A.K., De Ridder, N., Stroosnijder, L., Prins, H.H.T., 2002a. Fine-scale spatial distribution of plants and resources on a sandy soil in the Sahel. *Plant and Soil* 239, 69–77.
- Rietkerk, M., Boerlijst, M.C., Langevelde, F., HilleRisLambers, R., Van de Koppel, J., Kumar, L., Prins, H.H.T., Van de Ross, A.M., 2002b. Self-organization of vegetation in arid ecosystems. *Am. Nat.* 160, 524–530.
- Ritchie, M.E., Olff, H., 1999. Spatial scaling laws yield a synthetic theory of biodiversity. *Nature* 400, 557–560.
- Shannon, C.E., 1948. A mathematical theory of communication. *Bell Syst. Tech. J.* 27, 379–423.
- Shannon, C.E., Weaver, W., 1949. *The Mathematical Theory of Communication*. University of Illinois Press, Urbana.
- Sirkou, D., Alados, C.L., Papanastasis, V.P., Vrahnakis, M.S., Iovi, K., Giner, M.L., Ispikoudis, I., 2003. Assessment of grazing effects on the Mediterranean shrubs *Phillyrea latifolia* L. and *Cistus monspeliensis* L. with developmental instability and fractal dimension. *J. Med. Ecol.*
- Solé, R.V., Manrubia, S.C., 1995. Are rainforests self-organized in a critical state? *J. Theor. Biol.* 173, 31–40.
- Solé, R.V., Alonso, D., McKane, A., 2002. Self-organized instability in complex ecosystems. *Philos. Trans. R. Soc. Lond. B.* 357, 667–681.
- Soro, A., Sundberg, S., Rydin, H., 1999. Species diversity, niche metrics and species associations in harvested and undisturbed bogs. *J. Veg. Sci.* 10, 549–560.
- Sousa, W.P., 1984. The role of disturbance in natural communities. *Annu. Rev. Ecol. Syst.* 15, 353–392.
- Sugihara, G., May, R.M., 1990. Applications of fractals in ecology. *Tree* 5, 79–86.
- Tilman, D., 1994. Competition and biodiversity in spatially structured habitats. *Ecology* 75, 2–16.
- Tomaselli, R., 1981. Main physiognomic types and geographic distribution of shrub systems related to mediterranean climates. In: Di Castri, G., Goodall, D.W., Specht, R. (Eds.), *Mediterranean Types shrublands. Ecosystems of the World* 11. Elsevier Scientific Publishing Company, Amsterdam, The Netherlands, pp. 123–130.
- Troumbis, A.Y., Memtsas, D., 2000. Observational evidence that diversity may increase productivity in Mediterranean shrublands. *Oecologia* 125, 101–108.
- Tutin, T.G., Heywood, V.H., Burges, N.A., Moore, D.M., Valentine, D.H., Walters, S.M., Webb, D.A., 1972. *Flora Europaea*. Cambridge University Press, Cambridge.
- Van de Koppel, J., Rietkerk, M., 2000. Herbivore regulation and irreversible vegetation change in semiarid grazing systems. *Oikos* 90, 253–260.

- Wang, M.C., Uhlenbeck, G.E., 1945. On the theory of the Brownian motion. *Rev. Mod. Phys.* 17, 323–342.
- Whittaker, R.H., 1977. Animal effects on plant species diversity. In: Tusen, R. (Ed.), *Vegetation and Fauna. Bericht Internationales Symposium Rinteln*, J. Cramer, Vaduz, pp. 409–425.
- Whilhelm, T., Brüggemann, R., 2000. Goal functions for the development of natural systems. *Ecol. Model.* 132, 231–246.
- Wu, H., Sharpe, P.J.H., Walker, J., Penridge, L.K., 1985. Ecological field theory: a apatial analysis of resource interference among plants. *Ecol. Model.* 29, 215–243.